Call diversity in the North Pacific killer whale populations: implications for dialect evolution and population history

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Although killer whale (*Orcinus orca*) dialects have been studied in detail in several populations, little attempt has been made to compare dialect characteristics between populations. In this study we investigated geographical variation in monophonic and biphonic calls among four resident populations from the North Pacific Ocean: Southern and Northern Vancouver Island residents, southern Alaska residents, and eastern Kamchatka residents. We tested predictions about call variation across populations which are due to an accumulation of random errors and innovations by vertical cultural transmission. Call frequency contours were extracted and compared using a dynamic time-warping algorithm. We found that the diversity of monophonic calls was substantially higher than the diversity of biphonic calls for all populations. Repertoire diversity appeared to be related to the population size: in larger populations, monophonic calls were more diverse and biphonic calls were less diverse. We suggest that the evolution of both monophonic and biphonic calls is caused by an interaction between stochastic processes and directional selection, but the relative effect of directional selection is greater for biphonic calls. Our analysis revealed no direct correlation between call repertoire similarity and geographical distance. Call diversity within pre-defined call categories – types and subtypes – showed a high degree of correspondence between populations. Our results suggest that dialect evolution is a complex process influenced by an interaction between directional selection, horizontal transmission and founder effects. We suggest several scenarios for how this might have arisen and the implications of these scenarios for call evolution and population history.
Keywords: dialect, killer whale, acoustic repertoire, evolution, call type.

Vocal variation among groups of animals may occur at different levels. Variations in vocalisations between neighbouring groups of potentially interbreeding individuals are called dialects, whereas differences in acoustic repertoires over long distances and between populations that normally do not interbreed are referred to as geographic variation (Conner 1982). Dialects are common in birds (Baker & Cunningham 1985), but rare in mammals, being mostly limited to cetaceans (e.g., Ford 1991; Rendell & Whitehead 2003), bats (e.g., Boughman 1997; Esser & Schubert 1998; Yoshino et al. 2008) and humans (Labov 2001). In contrast, geographic variation in vocal repertoires is common among both bird and mammalian populations (e.g., Krebs & Kroodsma 1980; Slobodchikoff et al. 1998; Mitani et al. 1999).

Killer whales are widely distributed throughout the world's oceans (Forney & Wade 2007). Different populations display substantial variation in diet, behaviour, morphology and genetics (Ford et al. 1998; Pitman & Ensor 2003; Foote et al. 2009; Morin et al. 2010). Rather than being genetically coded, the vocal repertoire of killer whales is thought to be learned (Bowles et. al. 1988; Ford 1991; Deecke 2000; Foote et al. 2006), which leads to formation of dialects between neighbouring groups in some populations and geographic variation between distant populations.

As a species, killer whales feed on a wide variety of prey, but different populations often show a high degree of dietary specialization (Ford et al. 1998; Saulitis et al. 2000; Ford & Ellis 2006). In several regions, sympatric populations show little or no dietary overlap and represent different ecotypes (Ford et al. 1998; Saulitis et al. 2000; Pitman & Ensor 2003). Three killer whale ecotypes have been described from the North Pacific and these differ in social structure, morphology, genetics and behaviour: *residents* specialize on fish and live in large stable social units (Ford & Ellis 2006; Ivkovich et al. 2010), *transients* hunt primarily marine mammals and live in smaller more fluid social groups (Baird & Dill 1996; Ford et al. 1998), and *offshores* are probably fish specialists (Ford et al. 2011) and live in large groups with an unknown social structure.

Dialects have been described for several resident killer whale populations from the North Pacific (Ford 1991; Yurk et al. 2002; Filatova et al. 2007) and for killer whales from the northeastern Atlantic (Strager 1995). Resident killer whales from the North Pacific have a complex nested social structure comprised of 1) matrilines containing a matriarch and all her descendants, which always travel together; 2) pods containing a set of matrilines that associate frequently and use a common repertoire of stereotyped calls, which represents the vocal dialect of the pod; 3) acoustically distinct clans comprised of pods which share some repertoire calls; and 4) populations or communities containing one or more associating clans (Ford 1991; Ford 2002; Ivkovich et al. 2010).

Several distinct populations of resident killer whales have been identified in the North Pacific: Southern and Northern Vancouver Island residents, southern Alaskan residents in the northeastern Pacific (Ford 2002; Matkin et al. 1999), eastern Kamchatka residents in the northwestern Pacific (Ivkovich et al. 2010) and a number of less studied putative populations around the Aleutian and Kuril Islands and in the Bering and Okhotsk seas. Genetic and other research on these populations (Barrett-Lennard 2000; Hoelzel et al. 2002) has not, to date, provided detailed information about historical relationships among them.

It has been suggested that repertoires of stereotyped calls may serve as a marker of maternal relatedness. Divergence between vocal repertoires of killer whale pods is thought to happen gradually as pods grow bigger and matrilines spend less and less time together (Ford 1991). Vocal learning involves a series of call mistakes and innovations, which gradually make vocal repertoires diverge. For these reasons, Ford (1991) suggested a direct relationship between the maternal ancestry of different pods within clans and the degree of similarity of their vocal repertoires: the more distant the common maternal ancestry between pods, the fewer calls shared within their repertoires. This prediction was confirmed by Deecke et al. (2010), who showed that the similarity of one call type across matrilines was correlated with matriarch relatedness in spite of substantial male-mediated gene flow.

106 These findings suggest that populations with more recent common maternal ancestry
107 must have more similar repertories as well. Although killer whale dialects have been described in
108 detail in several populations, few studies have examined vocal variation between killer whale
109 populations. Yurk (2005) compared distribution of call syllables among subpopulations and
110 showed that distinct lower frequency syllables were shared between clans but differed between
111 populations, whereas upper frequency syllables varied between clans of the same population.
112 Foote & Nystuen (2008) showed that the frequency parameters of calls varied across ecotypes
113 (resident, transient and offshore). In this paper, we investigate the variation of whole frequency
114 contours across the three North Pacific resident killer whale populations.
115 Comparing killer whale acoustic repertoires is complicated by the fact that killer whale
116 sounds are not structurally homogenous. Killer whale sounds comprise several distinct structural
117 categories, common to all killer whale populations studied to date. Killer whale sounds include
118 whistles, echolocation clicks and pulsed calls. Most pulsed calls are highly stereotyped and can
119 be easily divided into call types (Ford 1991) with varying degrees of variability within types.
120 Many call types have an overlapping, independently modulated high-frequency component (Fig.
121 1); this phenomenon is usually referred to as "biphonation" (Wilden et al. 1998; Fitch et al.
122 2002) or, when two independent sources are responsible, "two-voiced calling" (Zollinger et al.
123 2008). Since the mechanism responsible for this pattern in killer whales is unknown, we use the
124 former term in this paper.
125 Biphonic sounds have been described in mammals as diverse as canids (Wilden et al.
126 1998; Riede et al. 2000, Volodin & Volodina 2002), primates (Fisher et al. 2001, Brown et al.
127 2003; Riede et al. 2004) and cetaceans (Tyson et al. 2007). While the functional significance of
128 biphonation in calls is not readily understood, its presence in the vocalisations of different
129 species suggests a potentially important communicative role. Proposed functions include the
130 enhancement of individual recognition (Aubin et al. 2000; Fitch et al. 2002; Volodina et al.
131 2006), or honest signalling of physical condition (Fitch et al. 2002). For killer whales, it has been

suggested that differences in the directionality of the lower- and higher-frequency components in biphonic calls can provide information on the orientation of a caller relative to a listener (Miller 2002). Differences in usage of biphonic and monophonic calls in diverse social contexts suggest that they may have distinct functions in killer whale communication with biphonic calls functioning mostly as group identifiers and monophonic calls serving as short-range contact signals (Filatova et al. 2009). Moreover, biphonic and monophonic calls show substantial differences in source levels (Miller 2006) and structure (Filatova et al. 2007), which suggests that they should be considered two distinct structural categories.

In this study we examined geographical variation in monophonic and biphonic calls among four resident populations from the North Pacific Ocean: Southern and Northern Vancouver Island residents, southern Alaska residents, and eastern Kamchatka residents (Fig. 2). We tested predictions about call variation across populations which are due to an accumulation of random errors and innovations by vertical cultural transmission. First, we compared the diversity of monophonic and biphonic calls within these populations. Second, we compared the similarity of monophonic and biphonic calls between each pair of populations. Finally, we measured call diversity within pre-defined call categories – types and subtypes, and examined whether call diversity within these categories differed across populations.

Methods

The study populations

Southern Vancouver Island resident killer whales (referred to below as SR) inhabit the coastal waters of British Columbia and Washington State. The core area of this population is in the waters of southern Vancouver Island, but they sometimes range south to Monterey Bay, California. The population consists of the single acoustic clan – J-clan (Ford 1991), which comprised 86 individuals in 2003 (van Ginneken et al. 2005).

Northern Vancouver Island resident killer whales (referred to below as NR) inhabit the coastal waters of British Columbia and southeastern Alaska, from southern Vancouver Island

158 north to southeastern Alaska (approximately 48°N to 58°N). The population is comprised of
159 three acoustic clans: A-clan, G-clan and R-clan (Ford 1991).
160 Southern Alaskan resident killer whales (referred to below as AR) range from
161 southeastern Alaska to Kodiak Island (Matkin et al. 1999) and possibly into the Aleutian Islands
162 and the Bering Sea (Allen & Angliss 2010). This population includes two acoustic clans: AB-
163 clan and AD-clan (Yurk 2002).
164 Eastern Kamchatka resident killer whales (referred to below as KR) were encountered
165 along the eastern coast of Kamchatka peninsula from Avacha Gulf to Karaginsky Gulf and east
166 to the Commander Islands. This population comprises three acoustic clans: Avacha clan, K19
167 clan and K20 clan (Filatova 2007).
168 Some overlap exists in the ranges of the northeastern Pacific populations: SR overlap
169 with NR in the waters of Vancouver Island, and NR overlap with AR in southeastern Alaska
170 (Ford et al. 2000). Despite this overlap, none of the populations have been observed to mix (Ford
171 et al. 2000).

172 **Data collection**

173 Sound recordings used for this study were taken from the existing long-term databases.
174 Recordings of Southern residents were made from 1980-2009, Northern residents from 1988-
175 1999, southern Alaskan residents from 1984-2008, and eastern Kamchatka residents from 2000-
176 2009. All recording systems had a flat frequency response from at least 0.1 to 7 kHz, although in
177 most cases this extended up to 20 kHz. We only included recordings that had sufficient
178 frequency bandwidth and signal-to-noise ratio to clearly display all call features.
179 The recordings were made from small (4-9 m) boats. Photographs were taken during all
180 recording sessions and compared to identification catalogues to confirm pod and population
181 identity, as described in Bigg et al. (1990).
182 In the recording sessions made directly for this study, all approaches to the whales were
183 conducted following procedures to minimize disturbance. To take photographs, the boat

184 approached at slow speed at 45° to the whale's course when they were traveling and left the
185 group immediately after the photographs of all group members were obtained. To make sound
186 recordings, we moved the boat 200-300 m ahead of the animals and waited until they passed us.
187 If the whales were feeding or milling, we stayed at a distance of 100-300 m from them to avoid
188 disturbing their natural behaviour. When the animals showed strong avoidance behaviour (e.g.
189 change in the direction of movement away from the boat), we stopped our activities and kept a
190 distance of at least 500 m from the group.

191 **Acoustic and statistical analysis**

192 We classified calls according to existing catalogues (Ford 1987; Yurk et al. 2002;
193 Filatova et al. 2004). For Alaska and Kamchatka, however, some call types were split and others
194 were added according to the results of more recent studies (see Filatova et al. 2007; Yurk et al.
195 2010). Two calls from each type/subtype were used for the analysis, with some exclusion of rare
196 call types for which we were not able to obtain at least two call samples of adequate quality. If a
197 call type had no subtypes, two samples from this call type were used. For call types that fell into
198 discrete subtypes, two samples from each subtype of this type were used. When possible, the
199 pairs of call samples from the same type/subtype were selected from different encounters and
200 different years to cover the presumed variation in the call structure. For calls which did not fall
201 into discrete subtypes but showed apparent group-specific variations (e.g., N12, see Ford 1991),
202 two calls from the opposite sides of the structural continuum were selected. In total, 348 samples
203 of 174 call types/subtypes were used for the analysis: 34 SR monophonic, 28 SR biphonic, 34
204 NR monophonic, 62 NR biphonic, 48 AR monophonic, 40 AR biphonic, 46 KR monophonic, 56
205 KR biphonic. Because our primary interest was call evolution, rare calls were of equal interest to
206 common calls, and we did not weight call similarities by the frequency with which each call
207 occurred.

208 Call contours were extracted using a custom-made MATLAB (The Mathworks, Inc.,
209 Natick, MA) routine for manually tracking frequency contours of each frequency component

(available online at www.russianorca.org/sound_pro.htm). After the operator selected enough points to track all modulations of the contour from the fundamental frequency and harmonics, the algorithm performed the generalization of frequency points by dividing them by the band number and joined them into a set of frequency measurements of the fundamental frequency, which were then smoothed and interpolated to produce a vector of frequency measurements with the sampling interval 0.01 s (Fig. 3). For biphonic calls, contours were extracted both from the low- and the high-frequency components. Calls were identified as biphonic if they contained the overlapping high-frequency component (Fig. 1).

Similarity of calls was measured using dynamic time-warping. Dynamic time-warping is an algorithm developed for the automated recognition of human speech that allows limited compression and expansion of the time axis of a signal to maximise frequency overlap with a reference signal (e.g., Itakura 1975). For this study, we used a modified version of the warping algorithm of Deecke & Janik (2006). Percent similarity of contours was calculated by dividing the smaller frequency value by the larger value at each point and multiplying by 100:

$$S(i) = \min [M(i), N(i)] / \max[M(i), N(i)]*100$$

where M is the reference contour and N the input contour. From the resulting similarity matrix, a cost matrix was constructed that kept a running tab on the similarities of the elements making up the curves while adding up these costs to give a final number called the "similarity" between the contours. In our algorithm, each element of the cost matrix was obtained by comparing the weighted sum of similarity values from two columns and two rows distant from the weighted diagonal.

Because the algorithm of Deecke & Janik (2006) only allows expansion or compression of the time axis by a factor of three, the algorithm cannot be used to compare calls that differ in length by more than a factor of three. In this case, their similarity is considered zero percent. This constraint biased the results in comparisons where many short or long contours were present in the repertoire of one population but not the other. To avoid this, we developed an

236 additional algorithm that stretched the shorter contour through interpolation to make it one point
237 longer than 1/3 of the longer contour.
238 For each pair of contours within each sample set, we measured their relative similarity in
239 frequency using this dynamic time-warping algorithm. By generating all possible pairwise
240 comparisons between call samples from sample sets, we used N samples to generate 0.5*N*(N -
241 1) comparisons. Since the correlation structure of this data set was unknown, we assumed that all
242 data points generated with the same sample were correlated. To achieve independence between
243 the analysis units, we calculated the mean similarity for each call sample and used it as the unit
244 of analysis for the further comparison.
245 For the measurements of ***intra-population call similarity***, we calculated the similarity
246 between each pair of calls from each major category (monophonic/biphonic) within each
247 population.
248 For the comparison of ***intra- and inter-population similarity of calls***, we calculated the
249 inter-population similarity for each pair of populations as a set of similarity values between each
250 call from the first population and each call from the second population. The median inter-
251 population similarity obtained by this method would depend not only on the true similarity
252 between populations, but also on the intra-population call similarity of each population. To get a
253 less biased inter-population similarity measure, we divided the median inter-population
254 similarity by the median of the pooled intra-population similarity values for each pair of
255 populations.
256 To measure ***call similarity within types and subtypes,*** we divided each of the six intra-
257 population sets of similarity values into the following three subsets: a) similarity values between
258 pairs of calls from the different types; b) similarity values between pairs of calls from the same
259 type; and c) similarity values between pairs of calls from the same subtype. To test for
260 differences in the type/subtype threshold between monophonic and biphonic calls, the combined

sets from all three populations were used. To test the differences in the type/subtype threshold across populations, subsets b) and c) were compared for the each pair of populations.

Statistical analysis was performed using R software (R Development Core Team 2010). Distribution of similarity values in most cases differed significantly from normal, so we used the non-parametric two-tailed Mann-Whitney U-test for all statistical comparisons. Bonferroni correction was applied in cases of multiple pairwise comparisons. A Mantel matrix permutation test (Schnell et al. 1985) was used to estimate the correlation of call similarity and geographical distance between populations. Distances were approximate based on the core summer distribution as the full extent of population ranges is unknown. In all statistical comparisons the significance level was accepted to be 0.05.

Results

Intra-population call similarity of monophonic and biphonic calls

We compared levels of similarity among monophonic calls with the levels of similarity among biphonic calls. Within each of the four populations, call similarity was significantly less among monophonic calls than it was among the biphonic calls in each population (monophonic vs biphonic, Mann-Whitney U-test, KR: $U = 109$, $N_1 = 46$, $N_2 = 56$, $p < 0.0001$; AR: $U = 89$, $N_1 = 48$, $N_2 = 40$, $p < 0.0001$; NR: $U = 98$, $N_1 = 34$, $N_2 = 62$, $p < 0.0001$) except SR in which the difference was close to significant ($U = 338$, $N_1 = 34$, $N_2 = 28$, $p = 0.051$). Differences between populations within these two categories were less pronounced (Fig. 4) though also significant in all cases except AR vs KR and NR vs SR monophonic, AR vs NR biphonic (Table 2).

SR had the highest median similarity (that is, the lowest call diversity) for monophonic calls followed by NR, AR and KR. KR had the highest median similarity for biphonic calls followed by AR, NR and SR. Including the higher-frequency component into the analysis of biphonic calls increased the call similarity within all populations (Table 1). In this case, KR again had the highest median similarity, followed by NR, AR and SR.

286 **Intra- and inter-population similarity of calls**

287 We compared intra- and inter-population similarity of monophonic and biphonic calls in
288 the each pair of populations (Table 3). Differences in intra- and inter-population similarity of
289 monophonic calls were non-significant for all comparisons. Intra-population similarity of
290 biphonic calls was significantly higher than inter-population similarity for all comparisons
291 (Table 3).

292 The fact that the inter-population similarity of monophonic calls did not differ
293 significantly from the intra-population similarity means that monophonic calls are equally
294 diverse within and between populations. For this reason we did not compare the inter-population
295 similarity of monophonic calls between pairs of populations.

296 Inter-population similarity of biphonic calls was the highest between AR and KR,
297 followed by KR-SR, NR-KR, NR-SR, SR-AR and NR-AR (Table 3). After dividing this value
298 by the intra-population similarity to obtain the "true" similarity measure, SR and NR were the
299 most similar, followed by NR-KR, SR-AR, AR-NR, AR-KR and SR-KR (Fig. 5A).

300 Inter-population similarity of biphonic calls compared by analyzing both the lower-
301 frequency and the higher-frequency components was the highest between KR and NR, followed
302 by KR-AR, SR-AR, NR-AR, SR-NR and SR-KR (Table 3). After dividing this value by the
303 intra-population similarity, SR and AR were the most similar, followed by NR-KR, AR-NR, SR-
304 NR, AR-KR and SR-KR (Fig. 5B). The correlation between approximate geographical distance
305 and call similarity measured by the lower-frequency component and by both the lower-frequency
306 and the higher-frequency components was non-significant (Fig.5).

307 **Call similarity within types and subtypes**

308 We measured the similarity between monophonic and biphonic calls from different types,
309 calls from the same type, and calls from the same subtype for each population (Table 4).
310 Similarities between calls from different types followed the pattern revealed by the comparison
311 of call similarities within populations: similarities between monophonic calls were significantly

312 lower than between biphonic calls ($U = 826$, $N_1 = 86$, $N_2 = 71$, $p < 0.0001$; Fig. 6). The
313 difference in similarity between monophonic and biphonic calls within types and subtypes was
314 non-significant. The differences in similarity of calls within types and subtypes across different
315 populations were non-significant.
316

317 ## Discussion

318 The comparison of monophonic and biphonic calls from the four North Pacific resident
319 killer whale populations revealed a pronounced difference in the degree of similarity between
320 monophonic and biphonic calls for each population. For all four populations, the diversity of
321 monophonic calls was higher than the diversity of biphonic calls. Differences between
322 populations in the diversity of call types from the corresponding category (monophonic or
323 biphonic) were less pronounced. This result suggests that monophonic and biphonic calls have
324 different principles of evolution that are shared among the different resident populations. This
325 supports the suggestion that monophonic and biphonic calls are discrete categories.
326 Our results are consistent with previous studies which found differences in source levels
327 (Miller 2006), directionality (Miller 2002) and usage (Filatova et al. 2009) between monophonic
328 and biphonic calls. Miller (2006) measured source levels of different killer whale sounds and
329 showed that monophonic calls exhibited mean source levels lower than biphonic calls. This
330 variation in intensity suggests that killer whale pulsed calls fall into two functional groups:
331 ‘‘long range’’ biphonic calls with a mean estimated active space of 10–16 km in sea state zero
332 and ‘‘short-range’’ monophonic calls with an active space of 5–9 km (Miller 2006). Miller
333 (2002) showed that the relative energy in the high-frequency components of biphonic calls was
334 significantly greater when animals were moving toward the hydrophone array than away from it.
335 It is likely that this difference could help listening whales to determine the direction of
336 movement of a caller. Filatova et al. (2009) showed that the proportion of biphonic calls in the
337 vocalisations of the eastern Kamchatka residents increased when more than one pod was present

338 in the area. The combination of these findings suggests that biphonic calls function mostly as
339 group identifiers and help whales to define group affiliation and monitor the position of group
340 members over long ranges. The function of monophonic calls is less clear, but, like killer whale
341 whistles (Thomsen et al. 2002), they may serve as short-range communication signals.
342 The similarity of diversity levels in monophonic and biphonic calls in four populations
343 raises the question of whether the repertoire structure in resident killer whales is genetically or
344 culturally inherited. It is now generally accepted that killer whales acquire the detailed structure
345 of stereotyped calls in their repertoire through vocal learning (Bowles et al. 1988; Ford 1991:
346 Deecke et al. 2000; Foote et al. 2006); however, other aspects of the vocal repertoire could be
347 innate. Many songbirds learn their songs from fathers or neighbouring males, but despite some
348 variation their song remains species-specific and retains a certain structure. Moreover, gradual
349 differences in the function, usage and raw structural difference of the songs versus calls appear
350 to be innate in songbirds (Marler 2004). The same is probably true for human languages:
351 although languages are learned and therefore extremely diverse, there is some inherited structure
352 common to all human languages (Pinker 1994; but see Evans & Levinson 2009).
353 The comparison of stereotyped call repertoires among populations produced rather
354 unexpected results. The classical theory of call change through random drift predicts that the
355 highest call similarity should occur in populations that are geographically close and therefore
356 may share the recent common ancestors. However, our analysis revealed no direct correlation
357 between call repertoire similarity and geographical distance (Fig. 5). There are several possible
358 explanations for this. First, it is possible that call evolution is too fast to be phylogenetically
359 meaningful on a population scale: call repertoires may be already so diverse that they retain no
360 signs of common ancestry, and all similarities could be the result of random convergence. It has
361 been suggested in resident killer whales that females choose mates with the most dissimilar
362 dialects (Barrett-Lennard 2000). This would drive sexual selection towards faster call evolution
363 to provide greater resolution in the recognition of kin (e.g., allowing discrimination between first

364 and second degree cousins). The opposite selection force may be caused by the need of killer
365 whale groups to possess markers of population identity. Biphonic calls of all three clans of the
366 eastern Kamchatka resident population have certain frequency features in common (Filatova et
367 al. 2007). In southern Alaska resident killer whales, distinct lower frequency syllables are shared
368 by clans within this population (Yurk 2005). In Northern residents, most stereotyped whistle
369 types are structurally identical in two of the three acoustic clans (Riesch et al. 2006). Northern
370 and Southern resident populations in British Columbia share a substantial part of their
371 geographical range but retain strong behavioural reproductive isolation, although it is not
372 obvious if the isolation is based on acoustic or other cues.
373 The interaction of these opposite evolutionary forces (diversifying and standardizing)
374 may lead to the “maximum diversity within the permitted range”, where the “range” is
375 represented by vocal population markers. This scenario is consistent with the fact that in our
376 study the diversity of biphonic and monophonic calls between populations was very similar to
377 that within populations, suggesting that every population had already reached some optimal level
378 of diversity for each call category. Moreover, the intra- and inter-population diversity of
379 monophonic calls did not differ significantly, suggesting that for monophonic calls the pressure
380 to standardise is lower.
381 It is interesting to note that the diversity of monophonic and biphonic calls appears to be
382 negatively correlated. This pattern is also related to the population size: monophonic calls are
383 more diverse and biphonic calls are less diverse in larger populations. Although the SR
384 population of about 86 animals (van Ginneken et al. 2005) is the smallest of the four populations,
385 it has the highest diversity of biphonic calls and the lowest diversity of monophonic calls,
386 followed by the NR with 216 animals (Ford et al. 2000), KR (650 individuals; T.V. Ivkovich
387 unpublished data) and AR (more than 1000 individuals; Allen & Angliss 2010). In human
388 languages, speaker population size was shown to be a significant predictor of phonemic
389 diversity, with a smaller population size predicting smaller overall phoneme inventories

390 (Atkinson 2011). Our results demonstrate that the diversity of monophonic calls follows the
391 same pattern as phonemic diversity in human languages, which suggests that their evolution is
392 driven by the same stochastic processes that also affect human phonemes (Labov 2001). By
393 contrast, diversity in biphonic calls shows the opposite pattern. This may be caused by the fact
394 that in larger populations the inbreeding risk is lower, and the need for unique vocal population
395 markers is higher, which shifts the balance of diversifying and standardizing forces in favour of
396 the latter. Therefore, we suggest that the evolution of both monophonic and biphonic calls is
397 caused by an interaction between stochastic processes and directional selection, but the relative
398 effect of directional selection is greater for biphonic calls.
399 An alternative hypothesis suggests that call similarity between populations does reflect
400 their ancestry, but the ancestry is not directly correlated with geographical distance. Killer
401 whales are highly mobile and phylogeographic structure could very easily be disturbed by long-
402 distance movements. For example, genetic studies showed that the resident killer whales of the
403 North Pacific are more related to the North Atlantic killer whales than to sympatric transient
404 populations (Morin et al. 2010). This suggests a complex and multi-stage history of population
405 formation and colonisation of the North Pacific Ocean. Moreover, the southern Alaskan resident
406 population possesses two haplotypes of the control region of mitochondrial DNA; one matches
407 with the single haplotype of the Northern resident population, the other with the single haplotype
408 of the Southern resident population (Barrett-Lennard 2000) and the eastern Kamchatkan resident
409 population (Hoelzel et al. 2007). It is possible that the AR population retains genetic diversity of
410 an ancestral population, while the NR, SR and KR populations have reduced diversity due to a
411 founder effect. Founder effects have been shown to reduce the diversity of syllables in bird songs
412 (Baker & Jenkins 1987) and phonemic diversity in human languages (Atkinson 2011). This is in
413 agreement with the reduced diversity in KR biphonic and NR and SR monophonic calls, but it is
414 in contradiction to the high diversity in SR biphonic calls. However, the information currently
415 available does not allow testing of this hypothesis, and further study of genetic and acoustic

similarity is required to reveal the population history of North Pacific killer whales. A comparison of repertoire similarity with mitochondrial haplotype similarity across populations can provide an important insight into population history and dialect evolution.

Similarities of biphonic stereotyped call repertoires measured by the low-frequency component and by both the low- and the high-frequency components were generally not consistent, although they agreed in some aspects (Fig. 5 A, B). It appears that the evolution of low-frequency and high-frequency components of biphonic calls is not always parallel, suggesting that it may be influenced by different factors. The inclusion of the high-frequency component in the analysis of the intra-population similarity always increased the similarity values (Table 1), indicating that the high-frequency component is less diverse within populations than the low-frequency component. It is possible that the high frequency component may be a more stable and reliable marker of population relatedness, than the more diverse and variable low-frequency component. Alternatively, the stability of the high-frequency component may be related to the radiation pattern of biphonic calls. The higher-frequency component is more directional than the lower-frequency component (Miller 2002), so it is clearly audible only when the signaller is orientated towards the receiver. Therefore, the more omnidirectional lower-frequency component would appear to be more useful for the long-range recognition of pod members. This may result in the higher contour variability in the lower-frequency component to make the call more discernible. Consequently, the type-specific variation in the contour shape of the higher-frequency component may be redundant because the call type is already identifiable by the lower-frequency component. In that case, the function of the higher-frequency component may be restricted to marking the orientation of a signaler while the lower-frequency component marks the pod membership.

The diversity of calls within type and subtype categories had a high degree of correspondence between populations, despite the fact that the initial categorisations were made by different researchers (Ford 1991; Yurk 2002; Filatova 2004). Unlike the graded vocalisations

442 of some other odontocetes (e.g., Weilgart & Whitehead 1990), killer whale pulsed calls are
443 highly stereotyped showing little variation within call types, but there are consistent differences
444 between them. Differences within type/subtype diversity between populations were non-
445 significant. Moreover, the difference in diversity between monophonic and biphonic calls was
446 non-significant within types and subtypes. This suggests that the observers had rather similar
447 ideas of what they meant by call type and subtype. No one has yet provided a satisfactory
448 definition of "call type" in killer whales, and the most common description of the categorisation
449 process refers to "the distinctive audible characteristics of the calls". Call structure changes
450 subtly but continuously over time (Deecke et al. 2000), and call type divergence is thought to be
451 a gradual process (Bigg et al. 1990; Ford 1991). Consequently, calls of different matrilines can
452 differ to a greater or lesser extent, and it is not always obvious where to place the border. Deecke
453 and Janik (2006) performed an automatic neural network categorisation of calls recorded from
454 North Pacific transient killer whales and identified 8 monophonic and 5 biphonic call types. Our
455 study provides an equally objective approach to call categorisation by comparing contours and
456 using a threshold similarity level to delineate call types.
457 In conclusion, our results suggest that divergence of vocal repertoires may not result
458 solely from the accumulation of random errors and innovations by vertical cultural transmission.
459 Repertoire diversity appears to be related to the population size: monophonic calls are more
460 diverse and biphonic calls are less diverse in larger populations. Call similarity across
461 populations does not correspond with geographical distance. All this suggests that dialect
462 evolution is a complex process subject to an interaction between directional and non-directional
463 agents of structural change. These may include opposing selecting forces to diversify and
464 standardise vocal repertoires, horizontal transmission of calls, as well as random drift.

465 ## Acknowledgements

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647 Table 1. Median time-warped frequency contour similarity (in %) between monophonic and
648 biphonic call types of different resident killer whale populations in the North Pacific, calculated
649 by the low-frequency component (LF) and by both low- and high-frequency components
650 (LF+HF).
651

	Population	Median similarity
monophonic	KR	45.75
	AR	46.58
	NR	54.47
	SR	55.01
biphonic LF	KR	72.16
	AR	66.38
	NR	65.08
	SR	60.55
biphonic LF+HF	KR	77.73
	AR	72.36
	NR	72.87
	SR	71.19

652
653

654 Table 2. Results of Mann-Whitney U-test comparison of intra-population call similarity of
655 monophonic and biphonic calls across different resident populations.
656

	Populations	U	N_1	N_2	p
monophonic	AR-KR	1068	48	46	0.789
	AR-NR	403	48	34	< 0.001
	NR-KR	322	34	46	< 0.001
	SR-NR	447	34	34	0.109
	SR-KR	416	34	46	< 0.001
	SR-AR	429	34	48	< 0.001
biphonic	AR-KR	606	40	56	< 0.001
	AR-NR	1205	40	62	0.814
	NR-KR	915	62	56	< 0.001
	SR-NR	345	28	62	< 0.001
	SR-KR	217	28	56	< 0.001
	SR-AR	292	28	40	< 0.001

657
658

659 Table 3. Results of Mann-Whitney U-test comparison of intra- and inter-population similarity,
660 median time-warped frequency contour similarity (in %) and "true" median similarity between
661 repertoires of different resident killer whale populations in the North Pacific.
662

		Mann-Whitney test				Similarity		
	Populations	U	N_{intra}	N_{inter}	p	Inter-population	Intra-population	"True" inter-population
monophonic	AR-KR	2188	94	48	0.771	45.62	46.23	NA
	AR-NR	1634	82	48	0.108	47.21	49.15	NA
	NR-KR	1727	80	46	0.569	49.12	48.41	NA
	SR-NR	909	68	34	0.080	52.31	54.66	NA
	SR-KR	1663	80	46	0.371	48.77	47.84	NA
	SR-AR	1717	82	48	0.227	46.72	48.80	NA
biphonic LF	AR-KR	2037	96	56	< 0.05	64.95	70.29	0.924
	AR-NR	1614	102	62	< 0.001	60.71	65.43	0.928
	NR-KR	2825	118	62	< 0.05	63.93	67.37	0.949
	SR-NR	1719	90	62	< 0.001	62.14	64.48	0.964
	SR-KR	1480	84	56	< 0.001	64.03	69.71	0.919
	SR-AR	837	68	40	< 0.001	60.76	64.70	0.939
biphonic LF+HF	AR-KR	1447	96	56	< 0.001	70.83	76.25	0.929
	AR-NR	1590	102	62	< 0.001	69.05	72.86	0.948
	NR-KR	2567	118	62	< 0.01	71.58	74.78	0.957
	SR-NR	1455	90	62	< 0.001	68.42	72.65	0.942
	SR-KR	647	84	56	< 0.001	68.01	76.33	0.891
	SR-AR	874	68	40	< 0.01	69.22	72.22	0.958

663
664

Table 4. Median and mean (in parentheses) time-warped frequency contour similarity (in %) between all calls within the vocal repertoire belonging to the different call types, between calls belonging to the same call type and calls of the same subtype for different resident killer whale populations in the North Pacific. For biphonic calls, similarity of the low-frequency component and both components combined are given separately.

	Population	different types	same types	same subtypes
monophonic	KR	44.99 (45.87)	89.19 (84.03)	91.40 (89.95)
	AR	45.53 (44.82)	90.44 (85.17)	91.83 (86.26)
	NR	51.40 (50.12)	85.34 (82.47)	90.79 (90.04)
	SR	53.51 (52.88)	91.56 (86.77)	92.84 (91.74)
biphonic - LF	KR	71.15 (68.34)	92.62 (91.26)	93.87 (92.04)
	AR	65.88 (63.61)	88.69 (84.4)	93.76 (92.17)
	NR	64.46 (64.97)	90.73 (89.1)	93.45 (91.45)
	SR	59.30 (57.16)	87.66 (76.44)	93.97 (91.26)
biphonic – LF+HF	KR	77.42 (75.05)	92.88 (91.43)	93.53 (92.51)
	AR	72.21 (70.97)	89.63 (89.66)	94.74 (93.97)
	NR	72.44 (71.74)	92.51 (90.69)	95.08 (92.58)
	SR	70.35	82.94	95.40

(69.25) (83.79) (93.35)

670

671

672 Figure captions

673 1. Spectrograms of monophonic (left) and biphonic (right) calls. Note the low-frequency
674 component (LFC) with multiple harmonics in both sounds and the high-frequency
675 component (HFC) which is not a multiple of the LFC in the biphonic call.

676 2. Map of the North Pacific Ocean showing the home ranges of the resident killer whale
677 populations investigated in this study.

678 3. Example of frequency contours extracted from the low-frequency component (LFC) and
679 the high-frequency component (HFC) of a K27 call from the eastern Kamchatka resident
680 population.

681 4. Intra-population time-warped frequency contour similarity between monophonic and
682 biphonic calls of four resident killer whale populations. Horizontal lines represent
683 medians, boxes interquartiles, and whiskers a 90% confidence interval.

684 5. "True" similarity (inter-population divided by intra-population time-warped frequency
685 contour similarity) of biphonic stereotyped call repertoires plotted by the approximate
686 geographical distance between four resident killer whale populations. (a) – similarity
687 measured by the low-frequency component; (b) - similarity measured by both the low-
688 and the high-frequency components.

689 6. Time-warped frequency contour similarity between monophonic and biphonic calls from
690 different types, from same types and from same subtypes. Horizontal lines represent
691 medians, boxes interquartiles, and whiskers a 90% confidence interval.

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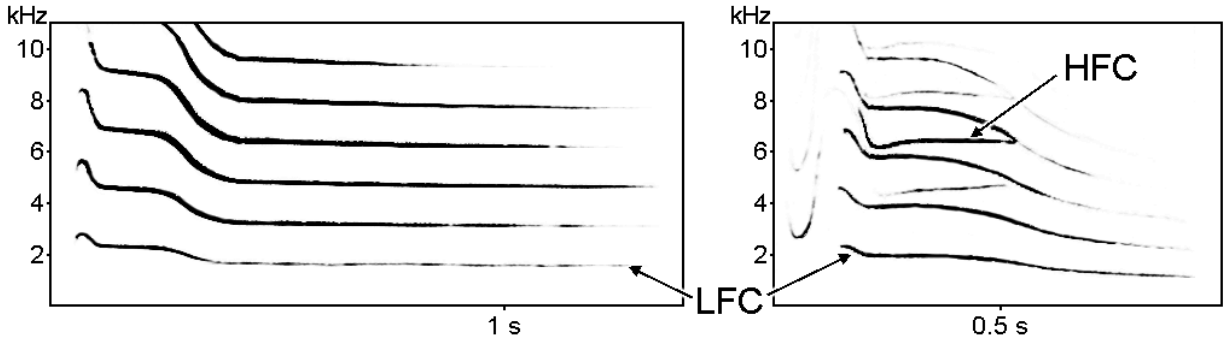

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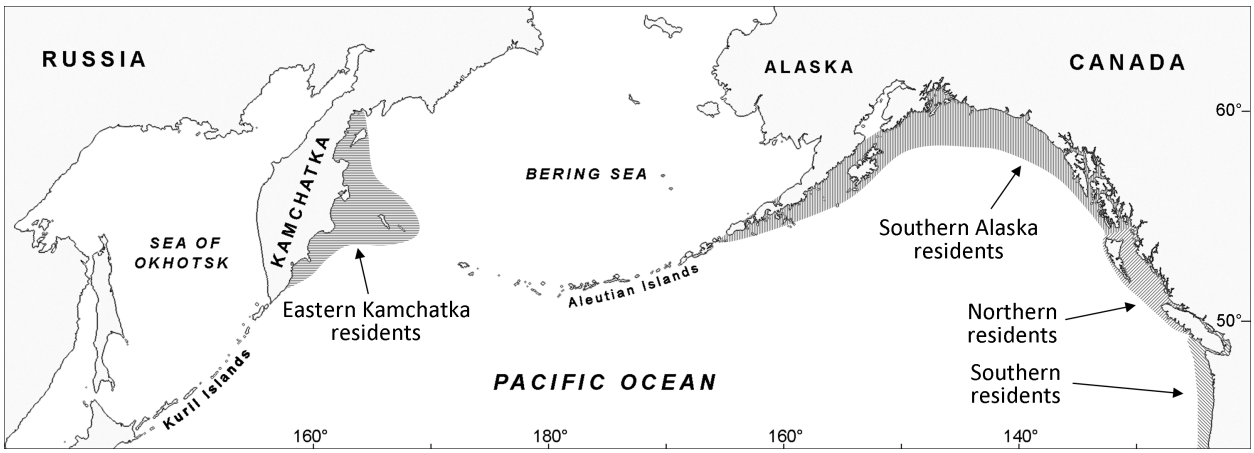
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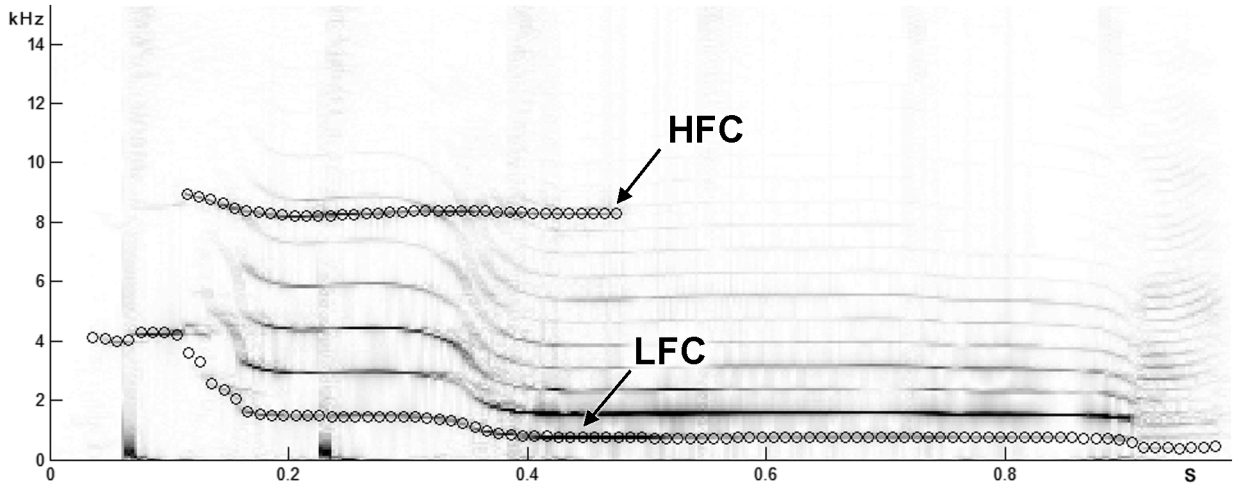

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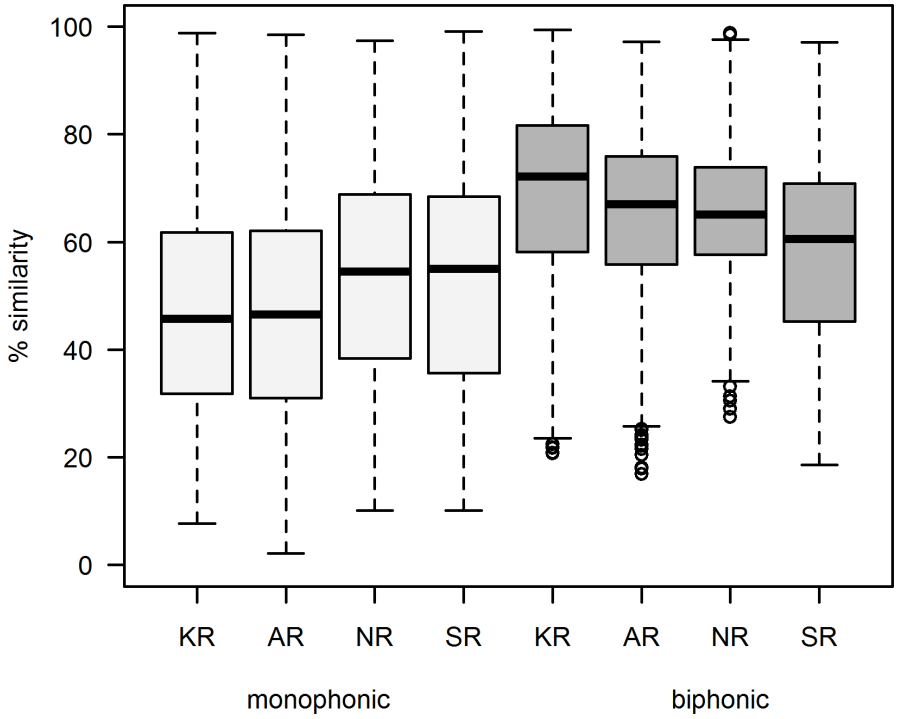
100
80
60
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% similarity
KR
AR
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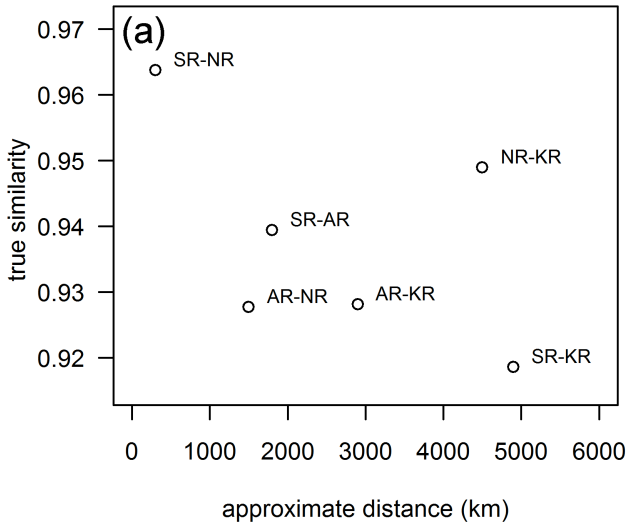
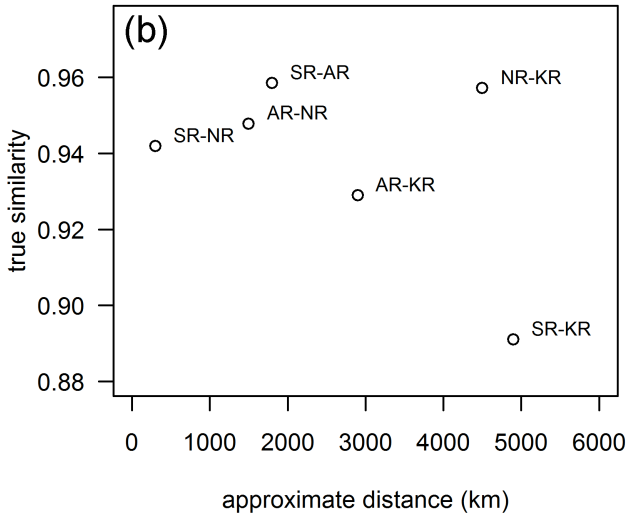
SR
KR
AR
NR
SR
monophonic
biphonic

700

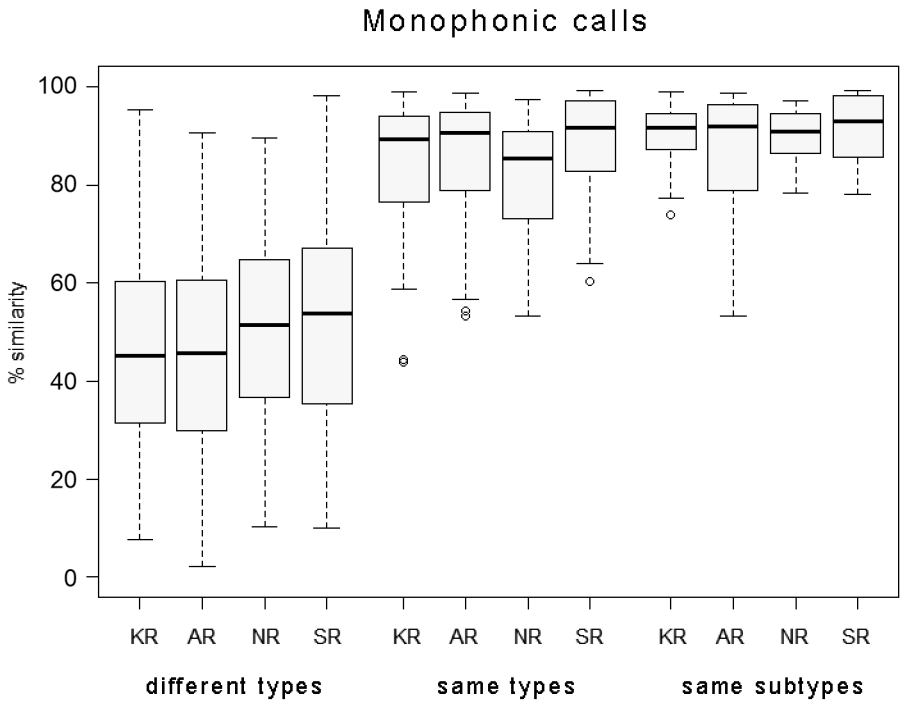
701

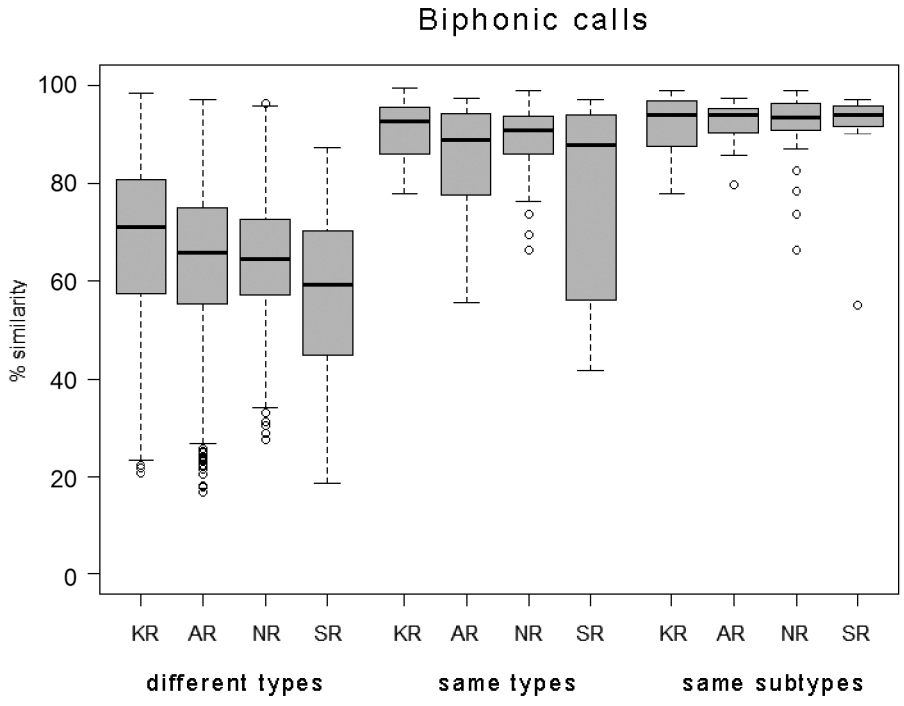

(a)
SR-NR
NR-KR
SR-AR
AR-NR
AR-KR
SR-KR
true similarity
0.97
0.96
0.95
0.94
0.93
0.92
0
1000
2000
3000
4000
5000
6000
approximate distance (km)


(b)
SR-AR
NR-KR
AR-NR
SR-NR
AR-KR
SR-KR
true similarity
0.96
0.94
0.92
0.90
0.88
0
1000
2000
3000
4000
5000
6000
approximate distance (km)

702

703


Monophonic calls
% similarity
100
80
60
40
20
0
KR AR NR SR KR AR NR SR KR AR NR SR
different types
same types
same subtypes


Biphonic calls
% similarity
100
80
60
40
20
0
KR AR NR SR KR AR NR SR KR AR NR SR
different types
same types
same subtypes

704